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# Genetic changes under domestication in *Vicia faba*

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**Summary.** The components of variation within each one of two sets of landraces and/or cultivars of *Vicia faba,* respectively constituted of primitive and advanced morphological types, were studied by means of two sets of 8×8 diallel crosses with two repetitions. The results show that primitive and modern forms differ from each other in both the intensity and the kind of selective pressures acting on them, mainly on those characters more modified through the domestication process: i.e., seed morphology and the number of flowers per node. Because of the paramount importance of the additive component in the primitive forms, it is suggested that the most important type of selection on them is the stabilizing one. On the contrary, in the most advanced forms the selection is directional and disruptive: directional towards greater yields, and disruptive separating two morphological types, 'major' and 'equina'. The plant response to these different selective pressures has been to modify the genetic control of different characters: thus the primitive forms generally show only additivity while the most advanced forms show additivity as well as directional and asymmetrical dominance.

**Key words:** Inheritance – Evolution – *Vicia faba* – Domestication

## Introduction

The adaptation of plants to man-modified environments involve changes in the genetic makeup of the original wild plants. These changes produce a continuum from primitive to modern cultivars with many intermediate degrees of domestication. Selection pressures can affect characters differently. They also can affect the same character differently depending on the material. Some existing studies describe the general changes brought about by domestication (Harlan 1975; Smartt 1978), and others describe genetic changes associated with qualitative characters that are controlled by major genes (Gladstones 1977; Blixt 1979) but very little attention has been paid to quantitative characters, even though most of the variation found in any population shows continuous variation.

We can reasonably expect that primitive and modern cultivars differ from each other in their genetic systems underlying some metric characters. As Mather (1973) pointed out, a stabilizing selective pressure will produce no or weak dominance variation; if the latter is the case, dominance will most likely be bidirectional. Contrarily, strong selective pressures will produce directional and/or asymmetrical dominance. Both directional and disruptive pressures must have played an important role in the initial processes of domestication in many crops (Doggett and Majisu 1968).

In the present paper we look at some aspects of the evolution of *Vicia faba* under domestication. Changes in plant structure have affected life cycle, plant height, branching pattern, flowers per raceme, pod length, seed size and shape, etc. In an attempt to order this morphological variation, Muratova (1931) recognized two subspecies, *faba* and *paucijuga.* The former is characterized by having more than two and one half pairs of leaflets per leaf and the less than two and a half. She split *faba* into three botanical varieties according to seed shape as measured by its thickness/length ratio: 'minor' (>0.70), 'equina' (0.70–0.26) and 'major' (<0.26). However, Hanelt (1972) merged *paucijuga* and 'minor' into ssp *minor,* because of their common seed features, maintaining two varieties, for ssp *faba faba* ('major') and 'equina'. However, considering the biological concept of species and Harlan and De Wet's (1971) system for cultivated plants, only one subspecies should be accepted in *V. faba* to which all the cultivated forms belong (Cubero 1974, 1984; Lawes 1980): the only candidate that constitutes a botanical variety is the Muratovan ssp 'paucijuga', because of its geographical isolation. The four latin names for the Muratovan entities as morphological types have been used here for practical purposes. Among these forms exhibiting clear primitive features can be found within 'pauci juga' (and also 'minor'), and forms exhibiting advanced characteristics can be found within 'major' according to the archaeological record. In a previous paper (Cubero and Suso 1981), we showed that the characters most influenced by domestication were those related to pod and seed, probably because selecting for greater yields has been the main and most consistent objective throughout the *V. faba* history (as a cultivated plant). Following in importance were the number of flowers per raceme and the leaflet density. More recently it has been suggested that the crucial point in the evolution of faba bean as a crop was when the flattened seeds (i.e. 'equina' and 'major' types) were obtained from rounded or subcilindrical ('minor' and 'paucijuga'). This change was probably due to genes acting on the mitotic orientation of the cotiledonary cells, and this was the only possibility for the plant to increase its seed size, hence, yield (Cubero 1984).

The present work studies the possible differences in the components of the variation in order to throw some light on the nature of the selective pressures that faba bean has suffered under domestication. In others words, how the domestication process has affected the primitive genetic systems. Up to now, the only well known fact, though not very precise, is that the large seeded cultivars originated from small seeded ones.

We will study here the components of the variation within each one of the two sets of cultivars, one formed by primitive, the second by more advanced, accessions.

The extensive studies on genetics of many quantitative characters performed by Cubero (1973) and Martin (1976), summarized in Martin and Cubero (1979), will be an excellent reference for us as crosses involving both primitive and modern types of cultivars were performed. Furthermore, these authors used two primitive accessions that are also included in the present work. In a few cases, our results will also be compared with those of Hobbs and Burnett (1982), who studied different sets of diallel crosses respectively formed by European, Russian, and Afghan lines. Unfortunately, the aim of their study was not the changes produced by the evolutionary processes but the inheritance of several agronomical traits, and a comparison with our results can only be done for some characters. Other works have also only been concerned with genetics and it is difficult to make valuable comparisons.

## Materials and methods

### *Materials*

Eight primitive accessions, five of then classified as 'paucijuga', and three as intermediate 'paucijuga'-'minor', were crossed among themselves to form a 8×8 complete diallel cross that will be labeled here as "P" group. Because of their morphological features, these eight accessions are possibly the most primitive ones in our collection. The former five are possibly similar to the unknown wild ancestor. We formed a different diallel cross between eight accessions of the 'equina' and 'major' morphological types, all of Spanish origin, to avoid lack of adaptation to our environment. This 8×8 diallel cross will constitute the "F" group in our study; the F accessions represent here the modern or evolved forms. The P set of crosses constitute the "universe" of 'pauci juga' accessions present in current collections already evaluated. Thus, the results obtained for the P group can be considered as fully representative (or almost) of very primitive forms, at least while the number of 'paucijuga' accessions is not drastically increased. This is not an easy short term task. On the contrary, the F set of crosses represents only a portion of the total variability existing in modern forms and even including dozens of accessions in the study, it would have been impossible to have exhausted the variability of the faba bean modern cultivars. Thus, the estimates of variability for the F set obtained here will generally be of lesser value than those that could be obtained by enlarging the differences within the F group.

The following characters were studied: leaflets/leaf, rachis length, leaflet density (leaflets/rachis length), leaflet length, leaflet width, leaflet width/length, stems/plat, sowing-flowering period, flowers/raceme, pods/node, pods/plant, seeds/plant, seed length, seed thickness and seed thickness/length.

Tables 1 and 2 show the characteristics of the parental lines.

### *Methods*

Two repetitions of each one of the two diallel crosses were studied in the field. For the reproductive characters, one of the repetitions was eliminated because of a strong Orobanche attack, which affected it in the last stage of maturity.

As we were primarily interested in the amount and the kind of variation, we applied the analysis of variance of Hayman (1954). We will follow the Hayman notation: a-additivity; b-dominance, studied by mean of its components; b1-directional dominance, b2-asymmetrical dominance, b3-residual dominance; c-maternal effects; d-reciprocal effects.

Additive and dominance effects were tested respectively against maternal and reciprocal effects when the two latter were significant (Kempthorne 1956).

## Results

Tables 3 and 4 show the Hayman's analysis of variance.

### *1 Number of leaflets per leaf*

P: additive, maternal and reciprocal effects were detected. F: additive and assymetrical dominance effects were significant. Martin and Cubero (1979) detected additivity and directional dominance of positive sense.

### *2 Rachis length*

P: strong additivity, weak directional dominance and reciprocal effects were detected. F: only additive effects were significant. Martin and Cubero (1979) obtained significance for additivity, for the three components of

**Table 1.** Characteristics of the parental lines. "P" "group"

| Line | 171 | 172 | 626 | 635 | 636 | 637 | 638 | 625 |
|---|---|---|---|---|---|---|---|---|
| Leaflets/leaf | 5.46 | 3.92 | 4.47 | 3.92 | 4.24 | 4.70 | 4.28 | 4.64 |
| Rachis length | 6.05 | 4.25 | 6.87 | 5.31 | 6.77 | 7.59 | 6.10 | 5.97 |
| Leaflet density | 0.91 | 0.95 | 0.66 | 0.81 | 0.64 | 0.62 | 0.70 | 0.75 |
| Leaflet length | 5.40 | 5.80 | 6.78 | 7.29 | 8.53 | 8.51 | 6.47 | 6.60 |
| Leaflet width | 1.81 | 2.05 | 2.61 | 3.97 | 3.92 | 3.50 | 3.04 | 3.21 |
| Leaflet width/length | 0.33 | 0.35 | 0.39 | 0.53 | 0.45 | 0.41 | 0.47 | 0.49 |
| Sowing-flowering | 18.90 | 29.00 | 23.85 | 35.80 | 37.80 | 28.50 | 43.00 | 29.61 |
| Flowers/node | 2.04 | 1.15 | 3.33 | 3.80 | 4.36 | 3.90 | 3.83 | 4.95 |
| Stems/plant | 4.60 | 2.50 | 3.57 | 3.40 | 3.90 | 5.80 | 3.25 | 5.03 |
| Pods/plant | 46.80 | 19.00 | 17.80 | 15.40 | 37.80 | 53.80 | 13.00 | 31.20 |
| Seeds/plant | 112.20 | 52.75 | 36.60 | 47.20 | 114.80 | 143.00 | 29.50 | 78.60 |
| Pods/node | 1.18 | 0.80 | 0.67 | 0.63 | 1.53 | 0.72 | 0.70 | 0.78 |
| Seed length | 0.85 | 0.72 | 0.97 | 0.71 | 0.72 | 0.75 | 0.66 | 0.68 |
| Seed thickness | 0.57 | 0.54 | 0.62 | 0.56 | 0.59 | 0.66 | 0.49 | 0.52 |
| Seed thickness/length | 0.66 | 0.71 | 0.61 | 0.76 | 0.82 | 0.88 | 0.76 | 0.77 |

**Table 2.** Characteristics of the parental lines. "F" group

| Line | 143 | 142 | 116 | 113 | 119 | 26 | 115 | 114 |
|---|---|---|---|---|---|---|---|---|
| Leaflets/leaf | 4.90 | 4.02 | 5.61 | 6.12 | 4.87 | 3.92 | 4.51 | 5.33 |
| Rachis length | 6.32 | 5.69 | 7.25 | 7.58 | 8.11 | 7.20 | 7.40 | 8.48 |
| Leaflet density | 0.79 | 0.72 | 0.77 | 0.82 | 0.60 | 0.56 | 0.62 | 0.63 |
| Leaflet length | 5.88 | 5.71 | 7.26 | 6.67 | 6.71 | 6.37 | 6.45 | 6.90 |
| Leaflet width | 3.58 | 3.95 | 3.50 | 3.25 | 3.16 | 3.13 | 4.05 | 3.14 |
| Leaflet width/length | 0.62 | 0.70 | 0.48 | 0.49 | 0.46 | 0.50 | 0.63 | 0.45 |
| Sowing-flowering | 23.90 | 40.30 | 12.00 | 6.60 | 11.85 | 5.39 | 25.80 | 16.85 |
| Flowers/node | 5.20 | 5.86 | 4.21 | 4.24 | 4.50 | 5.40 | 4.56 | 4.77 |
| Stems/plant | 4.22 | 2.90 | 4.45 | 4.42 | 5.12 | 4.20 | 4.60 | 3.97 |
| Pods/plant | 7.20 | 3.60 | 4.25 | 4.40 | 7.00 | 3.00 | 1.00 | 6.40 |
| Seeds/plant | 18.80 | 9.20 | 14.00 | 26.20 | 19.20 | 8.20 | 2.33 | 17.20 |
| Pods/node | 0.37 | 0.86 | 0.28 | 0.39 | 0.69 | 0.34 | 0.59 | 0.93 |
| Seed length | 1.81 | 1.37 | 2.32 | 2.27 | 2.24 | 1.46 | 1.96 | 1.86 |
| Seed thickness | 0.70 | 0.73 | 0.85 | 0.85 | 0.82 | 0.77 | 0.77 | 0.81 |
| Seed thickness/length | 0.38 | 0.53 | 0.36 | 0.37 | 0.36 | 0.53 | 0.39 | 0.44 |

dominance (direction of positive sense, asymmetry, and residual) and for the reciprocal effects.

### *3 Leaflet density*

P: additive and directional negative dominance as well as reciprocal effects were detected. F: weak additivity and both maternal and reciprocal effects were significant. Martin and Cubero (1979) found significance for additivity and for the three dominance components (the directional component of dominance was negative).

### *4 Leaflet length*

P: strong additive and reciprocal effects were present. F: strong additive effects were also significant but here they were accompanied by directional dominance effects of a positive sense. Martin and Cubero (1979) found reciprocal effects together with additivity and the three dominance components; the directional component of dominance was positive.

### *5 Leaflet width*

P and F: additive and positive directional dominance effects were detected in both groups. Martin and Cubero (1979) found the same results as for leaflet length.

### *6 Leaflet width/length*

P: the following effects were significant: asymmetrical and residual dominance, almost nil; additivity and maternal effects. F: additive, weak assymetrical dominance and maternal effects were present. Martin and Cubero (1979) detected only additivity and directional dominance of a negative sense.

**Table 3.** Analysis of the variance. Leaf and seed characters

| Character | Group | a | $b_1$ | $b_2$ | $b_3$ | b | c | d | Error |
|---|---|---|---|---|---|---|---|---|---|
| D.F. | | 7 | 1 | 7 | 20 | 28 | 7 | 21 | 63 |
| Leaflets/leaf · $10^{-2}$ | P | 245.05* | 63.27 | 29.75 | 17.03 | 21.86 | 36.18*** | 22.61*** | 7.23 |
| | F | 202.53*** | 0.74 | 39.99*** | 7.05 | 15.06** | 3.82 | 7.58 | 5.74 |
| Rachis length · $10^{-2}$ | P | 867.68*** | 834.93* | 129.78 | 83.76 | 122.09 | 80.68 | 102.90* | 49.29 |
| | F | 188.15** | 99.31 | 95.05 | 32.08 | 50.22 | 75.76 | 52.56 | 53.32 |
| Leaflet density · $10^{-2}$ | P | 6.34*** | 4.10** | 0.47 | 0.53 | 0.64 | 0.14 | 0.48* | 0.26 |
| | F | 4.62* | 1.30 | 0.60 | 0.93 | 0.33 | 0.67** | 0.40* | 0.20 |
| Leaflet length · $10^{-2}$ | P | 550.03** | 1,323.31 | 57.81 | 76.54 | 116.38 | 36.50 | 72.25** | 44.29 |
| | F | 151.70*** | 238.73*** | 12.64 | 33.09 | 35.32* | 15.43 | 19.28 | 19.62 |
| Leaflet width · $10^{-2}$ | P | 321.83*** | 299.34*** | 16.12 | 27.01 | 34.01*** | 19.57 | 18.25 | 16.01 |
| | F | 51.55*** | 70.20* | 17.86 | 17.60 | 19.55 | 24.00 | 19.43 | 12.42 |
| Leaflet width/length · $10^{-2}$ | P | 3.06** | 0.01 | 0.10* | 0.07* | 0.08** | 0.27*** | 0.04 | 0.03 |
| | F | 2.89** | 0.06 | 0.59* | 0.12 | 0.23 | 0.24*** | 0.20 | 0.15 |
| Seed length · $10^{-2}$ | P | 3.06*** | 0.96* | 0.13 | 0.21 | 0.21 | 0.19 | 0.15 | 0.51 |
| | F | 74.75*** | 2.04 | 4.25*** | 0.95 | 1.81* | 0.63 | 0.72 | 9.42 |
| Seed thickness · $10^{-4}$ | P | 45.87* | 8.80 | 9.61 | 9.91 | 9.79 | 18.54 | 12.95 | 15.83 |
| | F | 238.95*** | 4.58 | 33.48 | 12.98 | 17.80* | 3.32 | 8.20 | 37.56 |
| Seed thickness/ length · $10^{-2}$ | P | 1.29*** | 0.07 | 0.27 | 0.07 | 0.13 | 0.06 | 0.12 | 0.25 |
| | F | 1.66*** | 0.27** | 0.08** | 0.03 | 0.05* | 0.05* | 0.02 | 0.22 |

* Significant at 5% level; ** Significant at 1% level; *** Significant at 0.1% level

**Table 4.** Analysis of the variance. Yield components

| Character | Group | a | $b_1$ | $b_2$ | $b_3$ | b | c | d | Error |
|---|---|---|---|---|---|---|---|---|---|
| D.F. | | 7 | 1 | 7 | 20 | 28 | 7 | 21 | 63 |
| Sowing-flowering | P | 425.76*** | 82.09 | 7.21 | 27.08 | 24.08 | 31.97 | 16.21** | 7.31 |
| | F | 1,456.25*** | 72.71 | 46.66 | 27.51 | 33.91 | 4.46 | 20.85* | 10.57 |
| Flowers/node | P | 10.35*** | 1.60* | 0.29 | 0.39 | 0.41 | 0.49*** | 0.20* | 0.11 |
| | F | 3.20*** | 0.79*** | 0.37** | 0.15 | 0.23* | 0.16 | 0.08 | 0.12 |
| Stems/plant | P | 4.51 | 17.28*** | 2.10 | 1.89 | 2.49* | 5.04** | 2.26 | 1.35 |
| | F | 4.70 | 10.53*** | 1.03 | 0.31 | 0.85 | 2.16** | 0.43 | 0.66 |
| Pods/plant | P | 500.83 | 593.54 | 420.96 | 702.59 | 628.29 | 623.85 | 492.36 | 568.32 |
| | F | 69.59** | 154.68** | 21.25 | 21.76 | 26.38 | 13.37 | 16.50 | 26.44 |
| Seeds/plant | P | 3,285.85 | 5,597.95 | 3,337.58 | 6,204.74 | 5,466.28 | 3,601.78 | 4,078.49 | 4,554.25 |
| | F | 310.86 | 19.97** | 181.34 | 241.71 | 286.82 | 178.43 | 165.82 | 237.12 |
| Pods/node · $10^{-2}$ | P | 5.76 | 4.16 | 14.53 | 15.54 | 14.88 | 23.67* | 8.09 | 12.58 |
| | F | 10.51* | 11.83 | 2.12 | 3.60 | 3.53 | 6.65 | 3.47 | 4.63 |

* Significant at 5% level; ** Significant at 1% level; *** Significant at 0.1% level

### *7 Sowing-flowering period*

P and F: additive variation and reciprocal effects were the only significant effects in both groups. Martin and Cubero (1979) found additivity and asymmetrical dominance. Hobbs and Burnett (1982) obtained additivity, directional and residual dominance for European lines and additivity as well as reciprocal effects for both Afghan and Russian lines. Gadheri et al. (1984) pointed out that for this character the degree of dominance is inversely related to the genetic distance. A decrease in genetic differences (which is the case within each one of the F and P groups) will lead to a parallel decrease in the degree of dominance and eventually to its elimination.

### *8 Flowers per node*

P: additive effects and a weak directional component of positive dominance are present as well as both maternal and reciprocal effects. F: important additive effects are also significant, as well as positive directional and asymmetric dominance. Martin and Cubero (1979) found additivity, the three components of dominance and maternal effects, and Hobbs and Burnett (1982) obtained identical results for Russian lines. The European lines showed only additivity and directional dominance, and the Afghan ones, additivity and an almost insignificant asymmetrical component of dominance.

### *9 Stems/plant*

P and F: additivity is obscured by the maternal significant effects. Dominance effects are directional and positive. Martin and Cubero (1979) found significance for additivity and reciprocal effects. Hobbs and Burnett (1982) found additivity and directional dominance for the Afghan, European and Russian lines; asymmetrical dominance for the Afghan lines, and residual dominance for the European ones.

### *10 Pods/plant*

P: none of the genetical effects were significant; the environmental effects covered them. F: additivity and positive directional dominance were found. The raw data suggest a tendency for the hybrids to produce more than their parents. Martin and Cubero (1979) found significance for additivity and the three components of dominance (directional dominance showed positive sense). Hobbs and Burnett (1982) obtained varying results depending on the origin of the plants: additivity was significant in all three cases, but for the Afghan lines there was a significant directional and residual dominance; for Russian lines, directional and asymmetrical dominance and for the European ones, only dominance asymmetry.

### *11 Seeds/plant*

This is very similar to the previous character, the only difference is that additivity is also obscured by the environment in the F group. The same comment about heterosis can be made here. Martin and Cubero (1979) obtained significant results for all the components (dominance was of a positive sense) except for the maternal effects, and Hobbs and Burnett (1982) found only additivity and directional dominance within each of their three groups.

### *12 Pods/node*

Only maternal effects in P and additivity in F were significant. Martin and Cubero (1979) obtained additivity as well as the three dominance components (dominance positive) and Hobbs and Burnet (1982) found in addition to additivity in their three groups, only residual dominance for Afghan lines and reciprocal effects for the Russian ones; the European group produced the same results as those obtained by Martin and Cubero.

### *13 Seed length*

P: additivity was practically the only significant effect, as directional dominance was almost nil. F: additivity and asymmetrical dominance were present. Martin and Cubero (1979) found additivity and both the directional (negative sense) and asymetrical components of dominance.

### *14 Seed thickness*

P: only additive genetic variation was found. F: the main effect was additivity; a weak negative directional dominance variation was also present. There are no references in the literature to the genetics of this character.

### *15 Seed thickness/length*

P: only additivity was detected. F: significant effects were additivity, both negative directional and asymmetric dominance and a weak maternal effect. Martin and Cubero (1979) detected additivity, negative directional dominance and reciprocal effects.

## Discussion

### *1 Components of genetical variability within and between primitive and advanced forms*

Table 5 summarizes our results together with those obtained by other authors in a very schematic way that allows for some comparisons, namely "P" versus "F" (our study) and "other" authors results versus "ours". We will discuss the results by considering the different components of variation.

*a) Maternal and reciprocal effects.* These are non-nuclear genetic effects. In the present work, the P set of cultivars showed more variation than the F ones. Reciprocal effects were the main cause of variation in this sense. The biological meaning of these effects are not easy to explain. They can depend on particular crosses (the reciprocal effects) or on specific cytoplasms (the maternal ones). Previous experience indicates that many maternal effects detected in F1 are diluted or disappear in the F2 and F3. Thus, the causal connection between item c of Hayman's analysis of variance (i.e. maternal effects) and stable genetic factors of cytoplasm needs has yet to be demonstrated. The same can

**Table 5.** Summary of the results

| | a | $b_1$ | $b_2$ | $b_3$ | c | d |
|---|---|---|---|---|---|---|
| Leaflets/leaf | (P) F, MC | MC | F | | P | P |
| Rachis length | P, F, MC | (P), MC | MC | MC | | (P), MC |
| Leaflet density | P, (F), MC | P, MC | MC | MC | F | (P), (F) |
| Leaflet length | P, F, MC | F, MC | MC | (MC) | | P, MC |
| Leaflet width | P, F, MC | P, (F), MC | MC | MC | | MC |
| Leaflet width/length | P, F, (MC) | MC | (P) (F) | (P) | P, F | |
| Sowing-flowering | P, F, MC<br>A, U, E | E | MC | E | | P, (F)<br>A, U |
| Flowers/node | P, F, MC<br>A, U, E | (P), F, MC<br>U, E | F, M<br>(A), U | (MC)<br>U | P, MC<br>U | (P) |
| Stems/plant | MC<br>A, U, E | P, F, (MC)<br>A, (U), E | A | E | P, F | MC |
| Pods/plant | F, MC<br>A, U, E | F, MC<br>A, U | MC<br>U, E | MC<br>(A) | | |
| Seeds/plant | MC<br>A, U, E | F, MC<br>A, (U), (E) | MC | MC | | MC |
| Pods/note | (F), MC<br>A, U, E | (MC)<br>(E) | MC<br>E | (MC)<br>A, E | | (P)<br>U |
| Seed length | P, F, MC | (P), (MC) | F, MC | | | |
| Seed thickness | (P), F | | | | | |
| Seed thickness/length | P, F, M | F, MC | F | | (F), MC | |

( ) Significant at 5% level. P, F: Present work; E, A, U: Hobbs and Burwett (1982); MC: Martin and Cubero (1979)

be said for reciprocal effects; they are, in fact, residues in the analysis of variance of the diallel table.

*b) Additivity.* We can nearly skip over this effect as it generally was highly significant. The exceptions are for P stems, pods and seeds per plant and for F pods/node, stems per plant and seeds per plant. This lack of significance does not imply the nonexistence of addivity, but the extraordinary importance of maternal and mainly environmental effects detected for these characters. It seems that the genetic differences within each one of the Hobbs and Burnett groups were greater than those existing within our two groups. In the case of the Martin and Cubero study, the material was deliberately chosen for its high variability.

*c) Dominance.* Here are the most interesting results for the purpose of our study. First of all, it can be easily seen (Table 5) that when crosses between primitive and modern cultivars are involved, all dominance components are significant for most of the charactes. The Hobbs and Burnett groups also produced less significant dominance effects than those obtained by Martin and Cubero (1979), clearly demostrating that the genetic variability detected is a consequence of the distinct lines used in the crosses. This expressed variability may not concern all the characters. For example, the Hobbs and Burnett Russian and European sets of cultivars produced as much variation as those obtained by Martin and Cubero, but only for flowers per node in the Russian set and only for pods/node in the European ones.

Also worth mentioning is the fact that in their study, Martin and Cubero found that directional dominance was the only significant component in two important Muratovan characters: leaflets/leaf and seed thickness/length. This was probably caused by the fact that the faba morphological type was obtained from the primitive one (more or less similar to the Muratovan 'paucijuga') by directional selection producing more leaflets/leaf (by accumulating dominants of positive sense) and more flattened seeds (by accumulating dominant genes of negative sense). Asymmetrical dominance was not detected in their study, but it certainly is found within our F set. This could indicate a separation of 'major' from 'equina' morphological types within the F group, as will discussed below. A residual component of the dominance was detected only when asymmetrical dominance was present. This was also found by Martin and Cubero (1979) but not exactly so by Hobbs and

Burnett (Table 5). If this result is confirmed in the future, it would mean that good, particular combinations (=high specific combining ability) mainly arise in faba bean when materials coming from the divergent wings of a disruptive process of selection are crossed with each other. Important for the purpose of the present work is the fact that residual dominance was practically non-existent in both sets of crosses, P and F (it was only significant for leaflet width/length in P).

A similar situation appears when comparing the asymmetrical dominance component with the directional. In most of the cases the latter seems to be a requirement for the presence of the former, probably meaning that a directional selection occurred first and then a disruptive process, splitting the more evolved group. In two characters (leaflets/leaf and seed length), asymmetrical but not directional dominance was detected, and only in the F group. With the modern cultivars, for these same two characters, there probably was no longer a directional but instead a disruptive process, or just simply the former was much less important than the latter. Important for the purpose of our work is that there was no asymmetrical dominance in the overall P group. On the contrary, the F set shows four cases of significant asymmetry, which will be discussed below: leaflets/leaf, flowers/node, seed length and seed thickness/length.

## *2 Consequences of the process of domestication in Vicia faba*

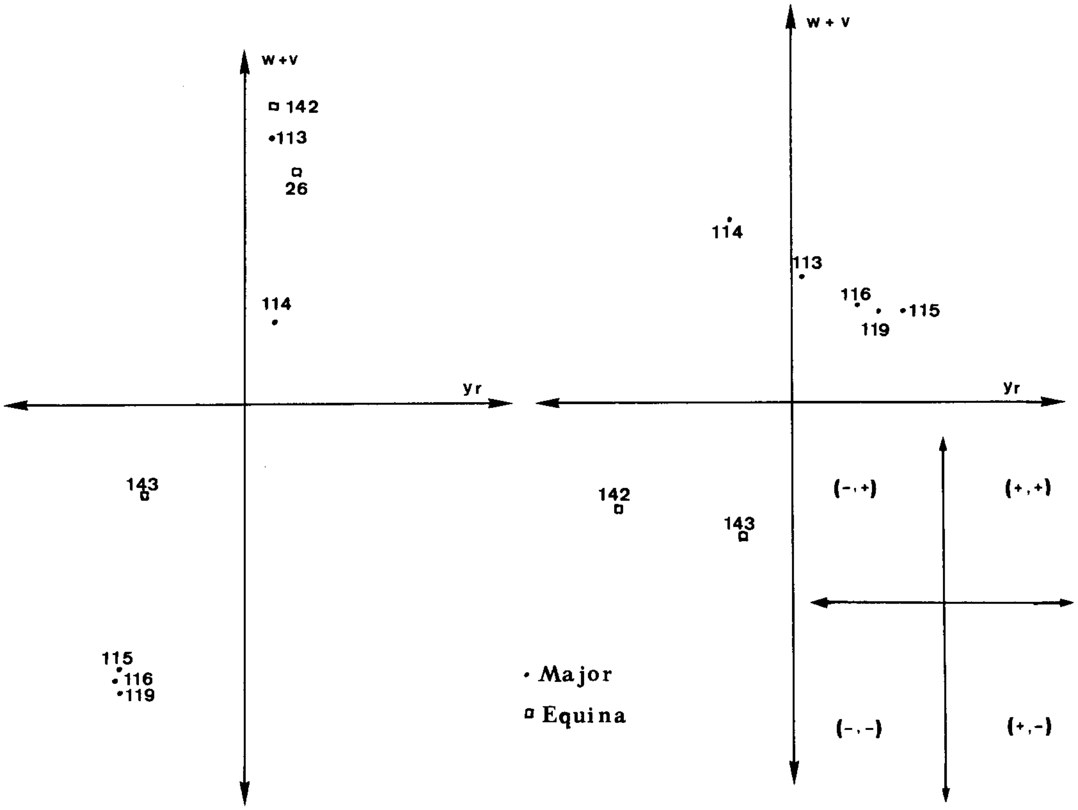
These differences between both groups, P and F, throws some light on the domestication process of *Vicia faba.* Although there are no signs of genetic differentiation within the P set of cultivars (most of the variation detected was additive), the F group has suffered a disruptive selection, as indicated by the asymmetrical component of dominance. This is detected in four taxonomically important characteristics splitting the whole group into two, namely the two morphological types 'equina' and 'major'. This disruption was probably a consequence of human activity, selecting 'major' from 'equina' because of its suitability for human consumption ('equina' is more flexible from the nutritional point of view but is mainly applied to animal feeding).

We must look further into this disruptive process within *faba* accessions. First, we will comment on the two seed characters, i.e., length and thickness/length. Figures 1a and b show the standardized parental averages plotted against the corresponding standardized dominance orders (W+V), obtained from the diallel analysis (the greater the W+V value, the greater the number of recessives; the smaller the W+V value the greater the number of dominants). For both seed characters, the dominant genes are negative and the recessive mostly positive. The 'equina' and 'major' types lie apart from each other in the case of seed length (Fig. 1a) but not so much in the case of thickness/length (Fig. 1b). But if we forget for a moment the taxonomical Muratovan items, 'equina' and 'major' and only consider morphological features, Fig. 1b shows that the genes having a positive effect lie in the recessive region and genes having a negative effect in the zone of dominants. Both figures, 1a and 1b, can be interpreted as follows: within the *faba* accessions, the proportionally thicker seeded types, showing greater values of thickness/length, are produced by recessive genes, as are the long seeded types. So then, a long and thick seed would require a huge amount of recessive genes, so many that, apart from physiological reasons as well as evident inverse genetic correlations, it would be difficult not only to obtain but also and to maintain in a partially outcrossed crop.

This pattern of variation is not at all visible in the case of the two other characters which showed asymmetric dominance, i.e. leaflets/leaf and flowers/node (Fig. 1b). Both dominants and recessives can be of positive and negative effects. This difference in the behaviour of these four characteristics can be explained if we consider the criterium of selection throughout the history of the crop, i.e. the pod morphology of *Vicia faba* and its reproductive system:

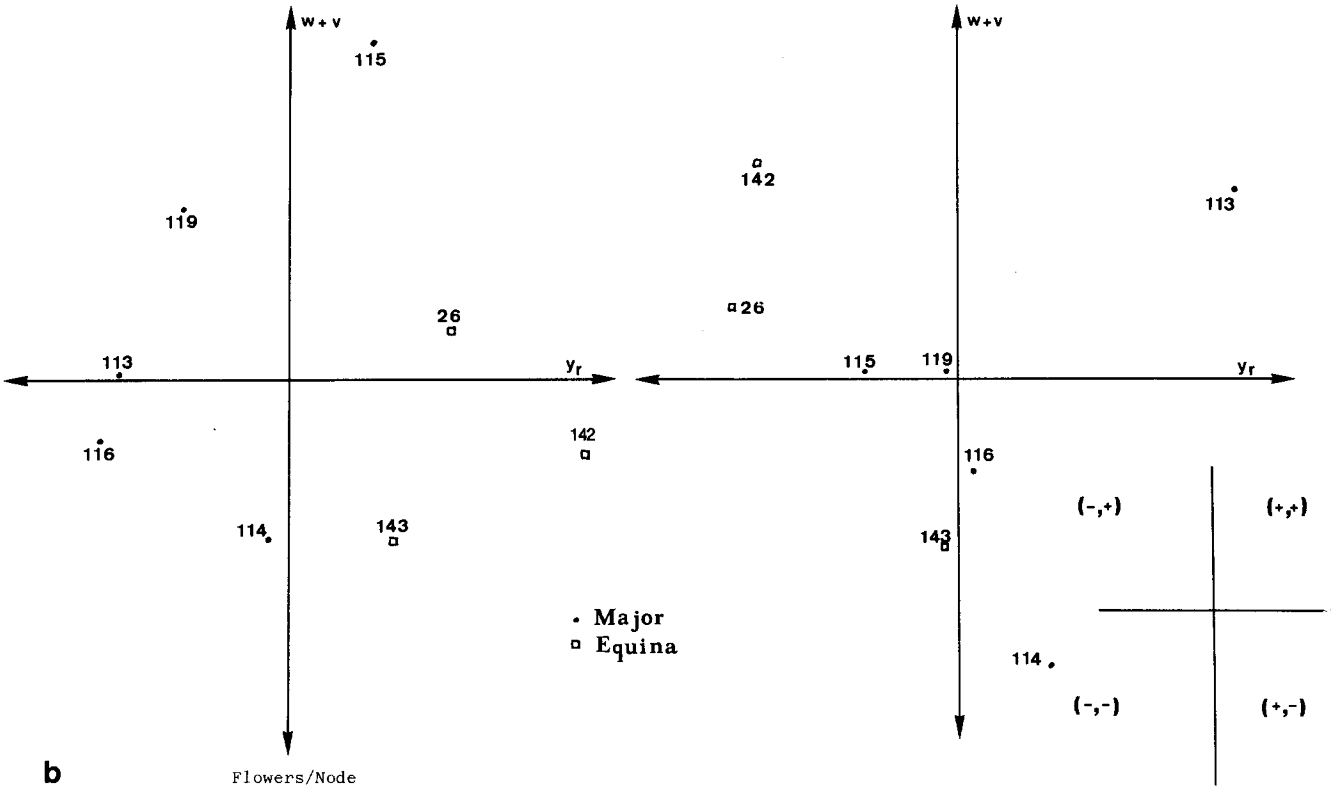
(a) The constant criterium for selection throughout *Vicia faba* history as a crop has been yield. It has been clearly shown by now that yield is related to seed size in faba beans, 'major' types being more productive than 'minor' (Bond 1984; 'paucijuga' is never included in agronomical trials). Man obtained *faba* types from the primitive ones, whose seeds were similar to the present day 'paucijuga' and 'minor' types as indicated by the archaeological record. This transition from primitive to *faba* types was a consequence of directional dominance. Our P set showed a very strong additive variation and a very weak directional dominance for seed length, but thickness and the ratio thickness/length only showed additivity. So then, the primitive populations were not split by differences in seed shape and size.

(b) By selecting for greater (=longer) seeds, man unconsciously "towed" a correlated character: flattened seeds, which are characteristics of both *equina* and *major* morphological types. Increasing the selective pressure for yield obligated the production of larger and, correspondingly more flattened seeds. As Cubero (1984) pointed out, obtaining flattened seeds allowed for an increase in seed size and yield because it is difficult to conceive how the pod would have had to change to contain rounded seeds weighing up to 2.5 g. In all herbaceous grain legumes, the largest seeds are



**a** Seed Thickness/length

Seed length



**b** Flowers/Node

Leaflets/ Leaf

**Fig. 1 a, b.** Parental averages and dominance orders always of a flattened "kidney" shape. An additional proof supporting that the selection was looking for more flattened seeds, even as an indirect consequence of selecting for higher yield, is provided by the fact that in the present work, the only seed character not showing significant asymmetrical dominance was seed thickness.

(c) Once these more productive *faba* types were produced, there were different but not necessarily divergent selection pressures. One of them aimed at higher yield and ended in landraces with really flattened and long seeds (i.e. the 'major' Muratovan variety) and another increased the seed size but not so much the fattening of the seed, i.e. the 'equina' Muratovan variety. Within the *faba* populations there was a disruptive process that separated dominants of negative effects from recessives of positive effects on seed size. As mentioned before, it would be very difficult to obtain large and rounded seeds because too many recessives in an outcrossed species would be required. During this evolutionary process, there was also a parallel variation in other characteristics, namely leaflets/leaf and flowers/node, both of taxonomical importance (leaflet density, which was an important character for Cubero and Suso 1981 in explaining total variation, seems to be a secondary character depending on the relative variation of its components, i.e., leaflets/leaf and rachis length). But it seems that they were not consciously selected by man. They also suffered a disruptive process, with dominant and recessive genes both able to show positive and negative effects. However, as there is not any recognizable variation, this asymmetry is better explained as a "correlated" asymmetry provoked by the selection of the main characters.

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